Tubucellaria : its Species and Ovicells.

By Arthur Wm. Waters, F.L.S.

(Plates 15 & 16.)

Collections made by Cyril Crossland, Esq., from the Red Sea, Zanzibar, and Cape Verde Islands contain species of *Tubucellaria*, and in one from Zanzibar sections have revealed several interesting points concerning the ovicells, about which nothing has been definitely known. It has therefore seemed advisable to deal with this genus at once, instead of waiting for the description of the collections upon which I am now at work.

The recent species *T. cereoides*, Ell. & Sol., and *T. hirsuta*, Lamx., are well known, and d'Orbigny described without figures another as *T. fusiformis*, to which I am able to add *T. zanzibariensis*, sp. nov. It will thus be seen that it is but a small genus occurring in the northern and southern temperates and the tropics, and also represented by a few species in the tertiaries of Europe and Australia.

There has been some uncertainty with regard to the specific names, but this is dealt with under the different species and it is to be hoped that the position will now be clearer.

It will be best to deal with the ovicell here, as there are various physiological facts of considerable importance to be noticed.

Busk * figured a tubular peristome curved inwards in *Tubucellaria hirsuta*, Lamx., but does not seem to have alluded to it. I † figured it in *T. cereoides* from Australia, and Reuss ‡ mentioned it in fossil *cereoides* from the Austrian Miocene, and, further, one was figured by me § in fossil *Porina papillosa*, Reuss. Levinsen ‖ in a most important paper has called these peristomial prolongations "peristomial oœcia," a name which had occurred to me when I was working on these ovicells, before recalling Levinsen's designation. Although Levinsen recognised their true nature, he gives no further particulars, but indicates that *Porina magnirostris* has similar ovicells. In my specimens of *P. magnirostris*, McG., there is no trace of ovicells, nor does this species seem closely allied to *Tubucellaria* in other particulars.

The ovicell which I figured in the peristome of specimens which I named *Porina coronata*, Reuss, is structurally allied to that of *Tubucellaria*. This, however, may have to be removed from *P. coronata*.

* Quart. Journ. Mic. Sc. vol. iii. p. 320, pl. 3. fig. 5, 1885.

† Ann. Mag. Nat. Hist. ser. 5, vol. xx. p. 190, pl. 5. fig. 10, 1887.

‡ "Foss. Bry. des Oest.-ung. Miocäns," Denkschr. math.-naturwissensch. kais. Akad. der Wissensch. vol. xxxiii. p. 147 (7), 1873.

§ Quart. Journ. Geol. Soc. vol. xlvii. p. 25, pl. 3. fig. 19, 1891.

‖ "Studies on Bryozoa," Vidensk. Medd. fra den Nat. Foren. i Kjöbenhavn, 1902.

In *T. cereoides* the end of this curved tube becomes gradually narrower, and the opening is small. The shape of the opening of the ovicell seems to be a specific character, for in *T. zanzibariensis*, sp. nov., the end of the tube is straight.

Many preparations of Mediterranean and other specimens have been made in the hope of finding an explanation of the meaning of these curved tubes, but without success, until it was at last revealed in a specimen from Chuaka, Zanzibar. There is some doubt whether this form should be called *T. cereoides* or should be separated specifically, as the ovicell is smaller than those seen in the Mediterranean specimens ; but at present we can hardly appreciate the value of the ovicellular characters, as so little work has been done in their investigation.

A number of serial sections have revealed most interesting and unexpected facts, but much remains to be made out, and sections are wanted of other species. The polypide (figs. 20, 25) is much modified, being thin and small, the tentacular sheath together with the diaphragm is extended, and passes as a tube through the oral aperture, past the operculum, to the end of the ovicell (figs. 18, 19) ; and near the diaphragm the lining membrane extends nearly across the opening of the ovicell, ending with a solid cover having a thick cuticula, under which there are some muscles ; and this expanded end, which at present I would call a plug, fits into a small notch at the opercular opening of the peristomial ovicell (fig. 18, see also figs. 20, 21, 25).

In order to understand the ovicell we should, before going further, examine the position of the tentacular sheath and diaphragm in the ordinary zoœcia. This diaphragm has been mentioned by Nitsche, Vigelius, Freese, Jullien (as irisoide), Pergens, Harmer (as vestibule), and by Calvet, who has given a *résumé* of the views of these authors. There seem, however, to be various points which have not been fully appreciated, and some of these may be found to be of use in determining the species. Longitudinal sections with the polypide withdrawn show the diaphragm looking somewhat like a contracted sac, which, in *Tubucellaria* and in many species of other genera, is situated at the side of the tentacular sheath as shown in fig. 15 ; in other cases it lies centrally in the tentacular sheath, as in *Myriozoum subgracile*, d'Orb., fig. 17, and here the mechanism is more easily followed, as part of the polypide has to pass through this diaphragm before the tentacles are spread out. The diaphragm or the tentacular sheath is attached on one side to the operculum, and on the other to the zoœcial wall (figs. 15, 16, 17), and this does not appear to have been generally understood—or, at any rate, explained. When the polypide is exserted a part of the tentacular sheath is carried with it, as shown diagrammatically in many text-book figures. It will be necessary to deal with these points in other species in subsequent papers.

In the ovicells of *Tubucellaria* the diaphragm is carried far beyond the opened operculum (*op*), and is attached by a continuation of the tentacular

sheath to the operculum (figs. 19, 20, 25). The polypide in the ovicellular zoœcia is, as already stated, very small, and is referred to as the diminutive polypide ; but although it is so small it is in full vigour, staining throughout and showing no signs of histolysis. The ring-canal, and the *so-called* ganglion, can be distinguished in this small polypide. Fig. 25 shows how it is formed from an ordinary polypide, for in *r* we still have the remains of the rectum, while part of the digestive tube (*dt*), namely the cardiac region, stomach, and cæcum, is separating into three cysts, or we may call them brown bodies, and other sections show the changes from the ordinary polypide to the diminutive in various stages. Fig. 25 is one of the most instructive sections, for we have the larva (*l*) in the ovicell and the ovarium immediately below the diminutive polypide ; and this is what we generally find, though in fig. 20 there are no larvæ, as they have probably been shed and another ovum will shortly pass into the ovicell. I have preferred to give fig. 20 as a copy of a section rather than to make it at all diagrammatic, though, in the stage figured, it is rather unusual not to find a larva in the ovicell, and a considerable number of sections show that the existence of the diminutive polypide with a larva in the ovicell and the ovarium immediately below it is no exceptional thing, but the general rule. Young ovaria occur in different places, but very frequently they are found in the neighbourhood of the upper lateral rosette-plate with parenchym-threads extending from the wall as in fig. 24.

In some Ctenostomata small polypides called "auxiliary polypides" * have been described, and these are formed in zoœcia which have previously contained an ordinary polypide, though now it has disappeared leaving only a brown body. The only function of these "auxiliary polypides" is said to be to eject the larva, and it is only natural to enquire whether the diminutive polypides of *Tubucellaria* have a similar function, though there is nothing to suggest this. In the first place, it is not a fresh polypide, but the original one modified ; then, in the second place, it seems as if the object were to get beyond the larva, for it is connected directly with the aperture of the ovicell. Probably we shall not obtain a full explanation until more species or living ones have been examined. If the object is to obtain direct communication with the exterior medium, could the spermatozoa be thus brought to the growing ova of the ovarium ?

In *Adeonella* there is a minute polypide at the distal end of the ovicellular zoœcium, and this will be dealt with shortly. The ovicell is rather like a Chinese puzzle, as there is one sac within another, and in the interior one the larva is developed. These calcareous species present great difficulties in study,

* Metschnikof, Bull. de l'Acad. de St. Pétersbourg, vol. xv. p. 507, 1871.

Nitsche, "Betracht. über die Entwicklungsgesch. und Morph. der Bry.," Zeit. für wiss. Zool. vol. xxii. p. 467, 1871.

Joliet, "Bry. des Côtes de France," Arch. de Zool. Exp. et Gén. vol. vi. p. 70, pl. 13. figs. 5–9, 1877.

as so much work is in the dark, for a suitable piece cannot be examined and chosen as in transparent species. However, it is to be hoped that further sections will elucidate some points still uncertain, and that we shall learn whether these polypides must be compared with those of *Tubucellaria*.

A more detailed examination of the ovicells of the Bryozoa is likely to reveal many new points: for instance, I find that the ovicell of *Thalamoporella Rozierii*, Aud., is double, and contains a larva in each division; also, the ovicell of *Idmonea radians* is compound, containing a group of larvæ in each of the four to six divisions.

It seems much the simplest plan to retain the old name "ovicell" as a general term, and then, instead of giving a special name for each kind of ovicell, to distinguish them by saying that the ovicell is a gonocyst, or that it is peristomial, and so forth.

TUBUCELLARIA CEREOIDES (*Ellis & Solander*). (Plate **15.** figs. 8, 9, 15, 16.)

Cellaria cereoides, Ellis & Solander, Zoophytes, p. 26, pl. 5. figs. B, C, D, E, 1786. See Miss Jelly's Catalogue, under *opuntioides*, for synonyms, though *Vincularia fragilis* of Defrance and of Blainville is not *Tubucellaria*, but add:—

Vincularia fragilis, Michelin, Icon. Zooph. p. 175, pl. 46. fig. 21, 1840.

Tubucellaria cereoides & var., MacGillivray, Tert. Polyzoa Victoria, p. 105, pl. 4. fig. 1, 1895.

Tubucellaria opuntioides, Calvet, "Bry. Mar. des Côtes de Corse," Trav. Inst. de Zool. de Montpellier, ser. 2, mém. 12, p. 11, 1902.

After Busk in the 'Challenger' Report had separated *T. cereoides*, Ell. & Sol., and *T. opuntioides*, Pallas, I followed him in using the latter name, although expressing my doubts as to the correctness of this separation. A further study of Busk's and of other specimens in the British Museum has convinced me that he was not right in the separation which he made; and now having another species, *T. fusiformis*, d'Orb., with which Pallas's description agrees much better, we must certainly retain Ellis and Sollander's name, which has so long been in use.

Busk's specimens of *T. opuntioides* are all from the John Adams Bank, N. Atlantic, and at first I thought that there might be differences of sufficient importance for separation, especially in the ridge at the base of the peristome, but having been permitted to make some preparations for the British Museum of the "*opuntioides*," I now consider that, so far as there are available characters, there is no material difference. In *Tubucellaria* the divisional wall is continued under the peristome (figs. 1, 8, 10), and in the John Adams Bank specimens this could hardly be made out until the covering membrane was removed. The specimen is less stout than is usual in the Mediterranean forms, and there are no large open pores round the peristome, though at the same time it is identical with some Mediterranean forms.

We thus have the *Tubucellaria cereoides* in its simplest form, with the peristomial ridge not very prominent, in the Atlantic; it occurs in its most

familiar form in the Mediterranean, while we get the variety *chuakensis* with the open spaces round the peristome further east ; but, contrary to Mr. Busk's statements, I do not find any material difference between the opercula of specimens from the Atlantic and of specimens from other localities. The operculum has a thickened bar across, a little above the middle, and that of *T. fusiformis* is similar. In the Naples specimens the bar is rather higher than in the others, and the state of preservation enables the oval opening in the membrane under the operculum to be more clearly distinguished.

There are about 27 tentacles.

It will be noticed in figure 8 that two series of tubular ovicells may occur together, but in the Naples specimens there is more frequently a series of ordinary zoœcia between the ovicells. In all cases the ovicells occur in groups all round the zoarium. In *Cellaria* and other genera the ovicells occur abundantly in parts of the zoarium and are absent from others.

There are a great number of delicate muscles attached to the compensation sac.

Loc. St. Paul's Rocks, N. Atlantic (*Chall.*) ; John Adams Bank ; Cape Verde Island ; Madeira ; Mediterranean ; Shubuk, Red Sea (24), collected by Crossland ; Manaar ; Loyalty Isles ; Torres Straits ; Queensland ; New South Wales ; Victoria ; South Australia ; Tasmania.

Fossil. Eocene, Miocene, Pliocene of Europe ; Victoria, Australia.

TUBUCELLARIA CEREOIDES, var. CHUAKENSIS nov. (Plate **15.** figs. 10–13, 18, 19 ; Plate **16.** figs. 20–25.)

Tubucellaria fusiformis, Busk (non d'Orb.), Zool. Chall. Exp. vol. x. p. 100, 1884.

It is with doubt that this is separated as a variety from *cereoides*, merely on account of the smaller beak-like ovicell, while there are no other characters of sufficient importance upon which separation can be based. However, as very few specimens with ovicells have been seen, and as it is important to record which form my sections refer to, I have called it a variety. There are large open pores or spaces round the peristome, and the ridge separating the peristome is very distinct; but in Mediterranean specimens these characters are found, though they are not generally so well marked. There are about 27 tentacles. The ovicells and larva have already been referred to.

In specimens from Grahamstown the ovicells are larger than those from Chuaka, but not so large as those from Naples, indicating that, unless additional characters are found, any separation of the *T. cereoides* group based largely on the size of the ovicell may not be ultimately retained.

Loc. Torres Straits (*Busk*), Brit. Mus. specimen 82.2.23.410 ; Grahamstown, South Africa ; Chuaka, Zanzibar, 3 fath., Mar. 29th, 1901 (512, 524), and Wasin, Brit. East Africa, 10 fath. (501), collected by Crossland.

TUBUCELLARIA FUSIFORMIS, *d'Orbigny*. (Plate **15.** figs. 1, 2, 3, 14.)

Tubucellaria fusiformis, d'Orb. Paléont. Franç. vol. v. p. 337.

Zoarium about 1 mm. in diameter, and at the end of each branch three fresh branches are given off attached by two or three corneous tubes. Occasionally there are also branches growing from the side of a branch. The divisional lines of the zoœcia can only be distinguished with difficulty even when the outer membrane is removed by eau de Javelle, or by other methods.

The zoœcia end in long peristomes, round the base of which there is a divisional line, and the surface of the peristome is ribbed, having one or two rows of pores between the ribs. The surface of the zoœcia is pitted all over and the peristomial pore is in a slightly projecting tube.

This form corresponds more nearly with Pallas's description of *Cellularia opuntioides* than any of the species recently thought to be *opuntioides*.

The specimen from Torres Straits to which Busk referred as *T. fusiformis*, d'Orb., in his 'Challenger' Report, p. 100, is a much stouter species with larger pores. To this I allude on p. 130. Harmer says that there is a *Tubucellaria* found by the 'Siboga' Expedition which is probably *T. fusiformis*, d'Orb. When passing through Paris I took the opportunity of examining d'Orbigny's specimen, which is only the basal portion of a lateral branch, and is only about the length of two zoœcia; an examination of this fragment, however, leaves me in no doubt as to the correctness of my determination. D'Orbigny described it as having "cellules sur quatre faces opposées"; which is correct for the basal zoœcia of the branches of *T. fusiformis*, but in the rest of the zoarium there are six zoœcia to a complete series.

Loc. Straits of Malacca (*d'Orb.*). There is a specimen unnamed in the British Museum (82.10.15.5.10) from Marie Louise, Amirante Is., Indian Ocean, 17 fath., collected by the 'Alert.' Chuaka, Zanzibar, 3 fath. (518); Wasin, Brit. East Africa, 10 fath. (520), collected by Crossland.

TUBUCELLARIA ZANZIBARIENSIS, sp. nov. (Plate **15.** figs. 4–7.)

Zoarium delicate, about 0·5–0·8 mm. diameter. It cannot be said that there are divisional lines, though the boundary of the zoœcia can often be traced in suitable preparations, and in the same way there is usually no line separating the peristome. There is a distinct suboral pore in a slightly raised tube, and the surface of the zoœcium is covered with elongated pits. The operculum is straight below, with a double chitinous wall on the distal border, covering a third of the operculum. There are 22–24 tentacles.

In a few nodes the peristomial ovicell is seen on most of the zoœcia; the ovicells are curved below, but with the terminal tubular portion straight, and the opening circular and as wide as the zoœcium; differing in these respects entirely from the peristomial ovicells of *T. cereoides* and *T. hirsuta*, Lamx.

The central branch is thicker than the lateral ones, which, however, are long and do not give off many branches; from the central one numerous long branches grow on all sides. There are only four zoœcia in a complete series, whereas in *T. cereoides* and *T. fusiformis* there are six.

The specimens were not in good condition for study, and no larvæ have been found in the peristomial ovicells.

Loc. Wasin, Brit. East Africa, 10 fath. (501); Ras Osowamembe, Zanzibar Channel, 10 fath. (504, 514); Prison Island, Zanzibar Channel (505); Chuaka Bay, Zanzibar, tow-net: all collected by Crossland.

Busk in his 'Challenger' Report, p. 99, refers to a species as *T. cæca*, but no description is given, and from examination of the British Museum specimens in the Busk collection I do not consider that it belongs to *Tubucellaria*.

D'Orbigny describes *T. clavata* from the Faluns bleu, but no figure is given and the description is insufficient.

Tubucellaria farnesinæ *, Neviani, also probably belongs to another genus.

T. marginata, MacG.†, fossil, looks like an erect form of his *Anarthropora* (*Lagenipora*) *tuberculata*, which I believe is the *A. horrida* of Kirkpatrick.

Onchopora ventricosa, *immersa*, and *granulosa* of Haswell‡ all have a wide sinus without projecting peristome, and do not belong to *Tubucellaria*.

EXPLANATION OF THE PLATES.

Plate 15.

Fig. 1. *Tubucellaria fusiformis*, d'Orb. From Chuaka, Zanzibar. × 12.
2. Do. Natural size.
3. Do. Operculum. × 85.
4. *Tubucellaria zanzibariensis*, sp. nov. × 12. From Ras Osowamembe, Zanzibar Channel (504). The upper part shows the peristomial ovicells, while in the lower part there are only ordinary zoœcia.
5. Do. Natural size.
6. Do. Operculum. × 85.
7. Do. Transverse section. × 25.
8. *Tubucellaria cereoides*, Ell. & Sol. × 12. From Naples, showing the peristomial ovicells.
9. Do. Operculum. × 25.
10. *Tubucellaria cereoides*, var. *chuakensis*. × 12. From Chuaka. Piece treated with eau de Javelle shows the peristomial ovicell on the left.
11. Do. Peristome. × 50.
12. Do. Operculum. × 85.
13. Do. Transverse section showing compensation-chamber. × 25.

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* "Bry. foss. delle Farnesina," Paleont. Ital. vol. i. p. 125, pl. 6. fig. 34, 1895.

† Tert. Polyzoa of Victoria, p. 105, pl. 4. figs. 2, 3.

‡ Polyzoa from the Queensland Coast, p. 36 (Linn. Soc. N. S. Wales, 1881).

Fig. 14. *Tubucellaria fusiformis*, d'Orb. Transverse section. × 25.

15. *Tubucellaria cereoides* (Ell. & Sol.). From Naples. Section showing the diaphragm (*d*) retracted; *op*, operculum; *ts*, tentacular sheath; *rs*, position of the rosette plate; *p*, polypide folded in the zoœcium. × 85.

16. Do. Section showing the diaphragm attached at one side to the operculum and at the other to the wall of the peristome. × 150.

17. *Myriozoum subgracile*, d'Orb. Section showing the diaphragm (*d*) with the polypide withdrawn. × 85.

18. *Tubucellaria cereoides*, var. *chuakensis*, var. nov. Section showing the peristomial ovicell containing a larva (*l*); also the diminutive polypide with the diaphragm (*d*) and the plug (*pl*) closing the ovicell. × 25.

19. Do. Section of the end of the diminutive polypide in the peristomial ovicell, showing the operculum (*op*) thrown back; further on the diaphragm (*d*), beyond which there is a growth, at the end of which the plug will ultimately be formed. × 250.

Plate 16.

Fig. 20. *Tubucellaria cereoides*, var. *chuakensis*, var. nov. Section through two ordinary polypides and two peristomial ovicells. This is an absolute copy of one section, though in two or three cases where the operculum had not been well cut through that detail had to be taken from the following section. In the peristomial ovicell the plug is seen withdrawn from the opening, but this may only be the result of decalcification and preparation, as changes are sure to take place when the calcareous support is removed. The operculum (*op*) has opened the peristomial ovicell for the passage of the diminutive polypide, and the position of the tentacular sheath (*ts*) and diaphragm (*d*) can be followed. In this case there is no larva in the ovicell, but apparently there has been one and the ovaria (*ov*) would probably soon furnish others. The parenchym passing through the rosette-plates is seen at *rp*. × 85.

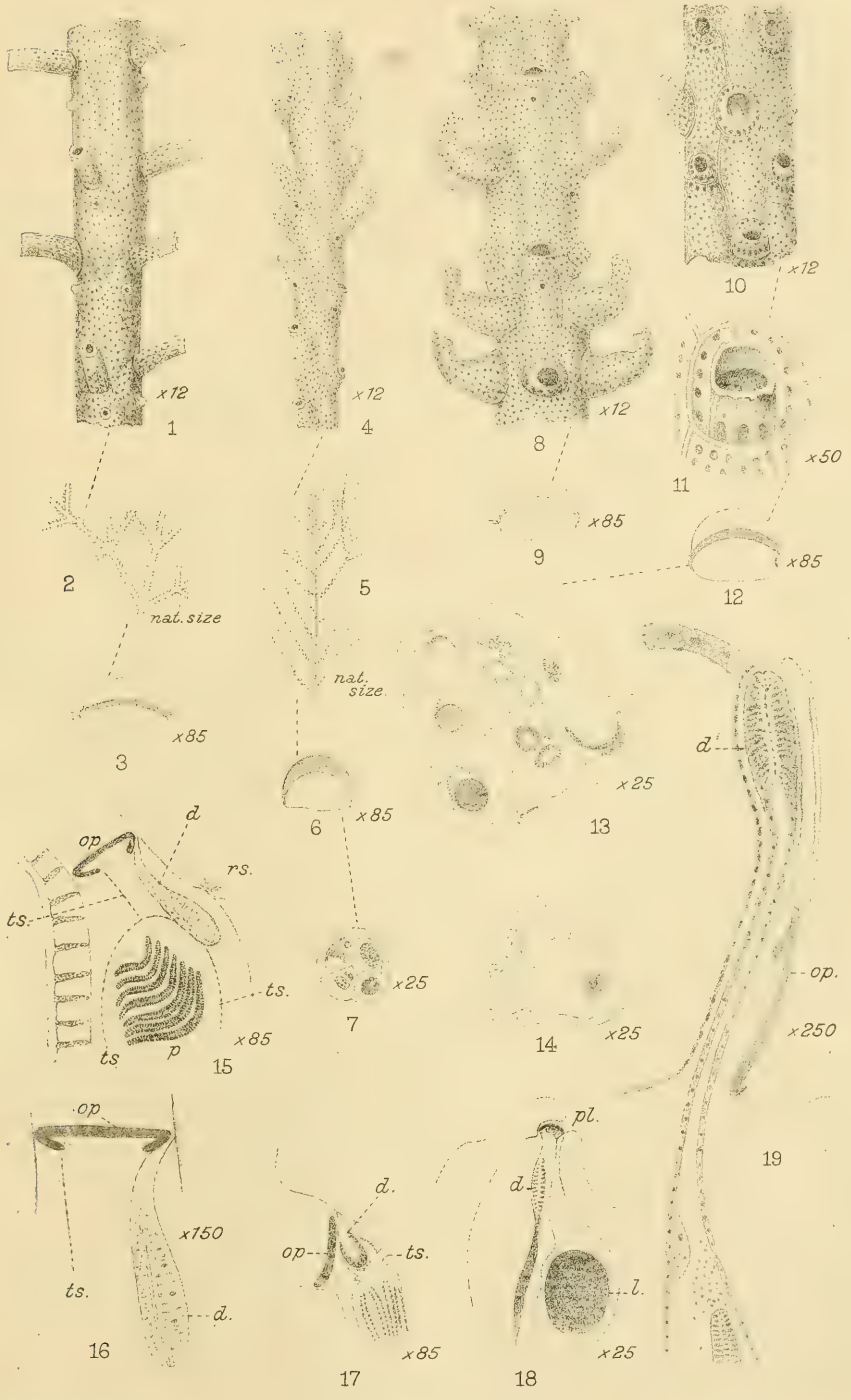
21. Do. Section of plug with diaphragm by the side. × 250.

22. Do. Section of larva. × 250.

23. Do. Section of the polypide-wall just past the operculum. In the lower zoœcia of fig. 20 these cogwheel cells are seen. × 250.

24. Do. Section of ovarium in the neighbourhood of a rosette-plate showing the protoplasmic network attached to the ovarium. × 150.

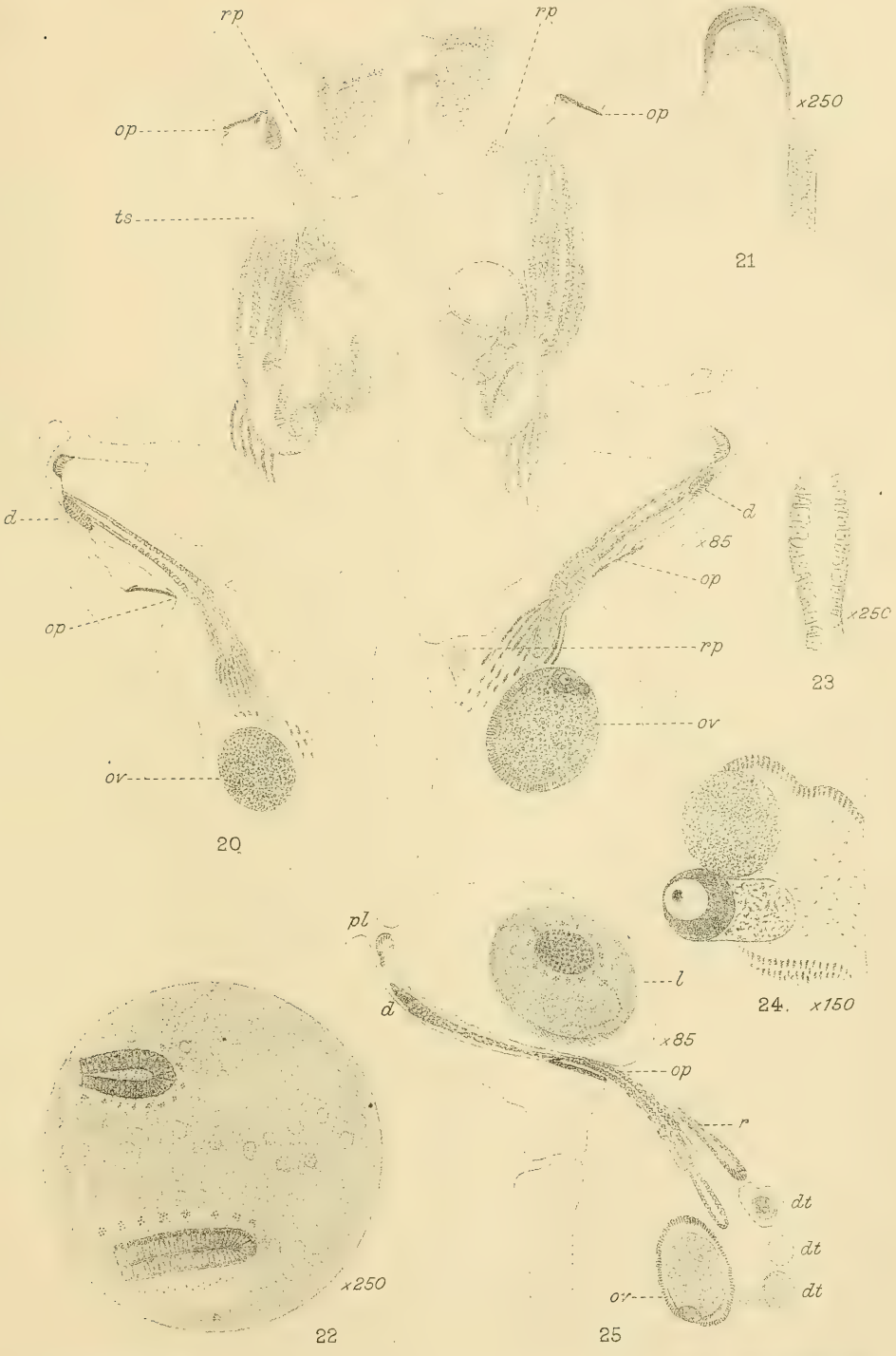
25. Do. Section of peristomial ovicell containing a larva. The diminutive polypide is shown and the plug (*pl*) to close the opening, also the remains of the rectum (*r*) and the incysting portions of the digestive tube (*dt*) are cut through. The ovarium (*ov*) is immediately below the diminutive polypide, and there are parenchym-threads from it to one of the cysts. This apparently shows an earlier stage than fig. 20, as we still have the indications of the complete polypide. × 85.



A. W. Waters del.
A. R. Hammond lith.

West, Newman imp.

TUBUCELLARIA.



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